GROWTH RESPONSE OF *CORTADERIA SELLOANA* AND *CORTADERIA JUBATA* (POACEAE) SEEDLINGS TO TEMPERATURE, LIGHT, AND WATER

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Abstract

Cortaderia selloana (pampasgrass) and *Cortaderia jubata* (jubatagrass) are South American perennial grasses species that have escaped cultivation in California and become aggressive invasive species, particularly in coastal environments. Both are characterized by large mounded tussocks, long serrated leaves, and feathery, plume-like inflorescences. While *C. jubata* is currently restricted to coastal areas in central and northern California, invasive populations of *C. selloana* can be found both along the warmer coastline of southern California and within interior regions of the state. To better understand the potential geographic distribution of these species in California we examined seedling growth responses to varying environmental factors, including light, temperature, and moisture conditions typical to both coastal and inland California sites. Under growth chamber conditions, both species grew optimally at 20°C. However, *C. selloana* seedlings had significantly greater height and leaf area compared to *C. jubata* at both 20 and 25°C. While temperature did not significantly affect *C. selloana* survivorship, mortality of *C. jubata* seedlings was ≥90% at temperatures above 25°C. Using shade cloth to control light intensity, *C. selloana* seedlings grew more vigorously than *C. jubata* under the higher light regimes, producing 234% more biomass at full sun. While the relative growth rate of *C. selloana* increased linearly with increasing light intensities, reaching a maximum of 21.4 mg g^{-1}day^{-1} at 1600 μmol m^{-2}s^{-1}, *C. jubata* growth rate reached a maximum of 12.7 mg g^{-1}day^{-1} at 60% full sunlight (960 μmol m^{-2}s^{-1}) and did not increase at higher light intensity. Drought significantly reduced growth of both species, but *C. selloana* was more tolerant of moderate drought than *C. jubata*. The mean dry weight of *C. selloana* seedlings was twice that of *C. jubata* when water was withheld for 27 days. When containers were maintained at varying ranges of soil moisture, *C. selloana* seedlings grew significantly taller and had higher leaf area and average dry weights than *C. jubata* at moderate drought conditions. The response to temperature, light, and moisture suggests *C. selloana* has greater potential invasiveness than *C. jubata* in both coastal and inland areas within the state, particularly in warmer regions. *Cortaderia selloana* growth was more vigorous then *C. jubata* under optimal conditions and also demonstrated greater drought tolerance and higher survivorship at increased temperatures and light intensity.

Key Words: California, *Cortaderia*, invasive, light, temperature, wildland.

Two South American species of *Cortaderia* have naturalized and become invasive in California. *Cortaderia selloana* (J.A. & J.J. Schult.) Asch. & Graebn. (pampasgrass) is native to Argentina, southern Brazil, and Uruguay, and *Cortaderia jubata* (Lemoine) Stapf. (jubatagrass, occasionally called pampasgrass or pin pampasgrass) is native to the Andes of Bolivia, Ecuador, and Peru (Connor and Edgar 1974). Both species cover extensive areas in their native range on plains, open slopes, and along river margins. They are large perennial grasses that form mounded tussocks of sharply serrated leaves with feathery, plume-like inflorescences that extend above the foliage on tall culms. The massive underground root structures are long-lived, reportedly surviving at least 40 years (Costas-Lippmann 1976).

In part because of their showy plumes, both species were introduced to California through the nursery trade in Santa Barbara in the mid 1800s (Costas-Lippmann 1977). *Cortaderia selloana* was planted more extensively than *C. jubata,* but both species have escaped cultivation and spread throughout the state. In addition to its ornamental uses, *C. selloana* (and possibly *C. jubata*) was planted by the Soil Conservation Service in Ventura County in the 1940s for erosion control and as supplemental dry land forage (Costas-Lippmann 1977). It has also been used for similar purposes in Australia, New Zealand, and Tasmania (Gadcil et al. 1984; Rawling 1988; Harradine 1991).

The primary physiological difference between the two species is their reproductive strategy. Populations of *C. jubata* consist of entirely female plants that produce seed apomictically (Conner 1972). In apomixis, seeds develop asexually without any pollination, resulting in seeds that are genetically identical to the parent plant. In contrast, *C. selloana* is functionally dioecious, producing

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seed through typical pollination of the female flowers (Conner 1972). Seed production is prolific in both species; Drewitz (2000) estimated that a single *C. jubata* inflorescence could produce up to 120,000 seeds. Airborne seeds are reported to disperse 20 miles in the wind (Harradine 1991).

Although it was widely recognized in the literature that *C. jubata* was an aggressive invasive weed, only recently has *C. selloana* been regarded as a widespread invasive species of wildlands (DiTomaso et al. 1999). Both species thrive on the California coast where fog is common, summertime temperatures are moderate, and winters are wet with little or no frost. Currently, *C. jubata* has a strictly coastal distribution in central and northern California. Invasive populations of *C. selloana* are concentrated along the warmer coastline south of Santa Barbara County (DiTomaso et al. 1999), but have been shown to have greater invasive potential than *C. jubata* (Lambrinos 2001). In addition to invading coastal habitats, *C. selloana* has also expanded its range into interior regions and has occupied a greater diversity of habitat types in California than *C. jubata*. In these warmer and drier interior climates, *C. selloana* can be found in wetlands, riparian corridors, and other waterways (Lambrinos 2001). Thus, we hypothesize that *C. selloana* is better adapted to higher light and temperatures compared to *C. jubata*.

Lambrinos (2000) attributed the invasiveness of *C. selloana* to its system of out-breeding and a greater ability to adapt to different selective regimes. Costas-Lippmann and Baker (1980) found significant allozyme variation across five different enzyme systems for *C. selloana* populations in California, but *C. jubata* did not exhibit any allozyme variation among populations. The greater genetic diversity of *C. selloana* may allow for more ecotypic flexibility and may contribute to its continued invasive success and ability to infest a wide variety of climates and habitats. In contrast, the apomictic strategy of *C. jubata* is likely advantageous in founding populations when colonizing new areas, because a single individual can produce copious seed. However, *C. jubata* has little opportunity for adaptation to new environments through genetic recombination. Consequently, the capacity for *C. jubata* to expand its range beyond its current coastal distribution may be limited, while *C. selloana* may be poised to expand within both inland and coastal regions.

Large populations of both species can displace native plants, impact wildlife habitat, reduce access to recreational areas and can become a significant fire hazard (Lambrinos 2000). They have also been shown to reduce conifer establishment and growth in logging operations (Fuller 1976; Gadcil et al. 1990). Because of their ecological impacts in natural areas, the California Exotic Pest Plant Council (currently California Invasive Plant Council) has listed both species among the most widespread invasive wildland plants in California (Howald et al. 1999). In addition to California, both *C. jubata* and *C. selloana* are also considered invasive in Australia, New Zealand, and South Africa (Rawling 1988; Harradine 1991).

The objectives of this study were to compare the growth responses of *C. jubata* and *C. selloana* seedlings to varying conditions of light, temperature, and moisture typical to both coastal and inland California conditions. From these results, we hope to better understand the environmental conditions that influence seedling establishment and potential geographic distribution of both species in California. These finding may have important implications for predicting where seedlings are likely to establish and where detection and prevention programs should be focused.

MATERIALS AND METHODS

Plant Material

For all *C. jubata* experiments, seeds were collected in California at Vandenberg Air Force Base (VAFB), Santa Barbara County and at Big Lagoon, Humboldt County. The seeds from VAFB were designated as a southern population and seeds from Big Lagoon a northern population. The experimental results from the two populations were not statistically different and only combined results are presented. *Cortaderia selloana* seeds used in the temperature experiments were collected at Vandenberg Village, near VAFB, and seeds used for the light intensity, drought, and moisture stress experiments were purchased from the Mistletoe Seed Company in Santa Barbara County.

For each experimental year, fresh plumes on mature plants were collected in the field the previous fall. Only seeds less than one year old were used for all experiments. Seeds were removed from the inflorescences, stored in paper bags in the laboratory at room temperature and used as needed.

Growth Conditions and Harvest Procedures

Temperature. Seeds were sown on the surface of Yolo Fine Sandy Loam (YFSL) in black plastic trays (51 holes per tray) on March 11, 2000. Plants were grown in the greenhouse under natural light and subirrigated daily with 5% Hoagland's solution. After one week, seedlings were thinned to one per hole and grown for an additional two weeks. Daily day/night greenhouse temperatures averaged 24 and 18°C, respectively, during this period. Twenty-one days after planting, three flats (one northern and southern *C. jubata* population, and one *C. selloana*) containing a variable number of plants were transferred to each of six controlled temperature rooms. Plants were grown in a growth chamber at constant temperatures of 10, 15, 20, 25, 32 or 37°C for two months under fluorescent bulbs set to a 12 hr photoperiod. Light levels averaged 75 μmol·m^{-2}·s^{-1}

photosynthetic photon flux density (PPFD) with no significant differences across all six chambers. Soil was kept moist with a weak nutrient solution.

A pretreatment baseline harvest was conducted using 6 to 8 replicates per flat, with individual plants serving as replicates. Measurements included plant height, number of leaves, and number of stem tillers, as well as the number of surviving seedlings. Plants were clipped at the soil surface and evaluated for leaf area with a LICOR Model LI-3100 Leaf Area Meter. Aboveground biomass was dried at 32°C for 2 wk and then weighed. Measurements were taken on the remaining plants every two weeks and all plants were harvested after 8 wk and evaluated as described above. Data are reported only for the 8-wk harvest timing.

Light intensity. For all greenhouse experiments, seeds were planted on the soil surface in one gallon black plastic pots filled with YFSL. Seedlings were thinned to one per pot and grown in a greenhouse of the Vegetable Crops Department at the University of California, Davis. Pots were irrigated as needed with tap water.

Light intensity in the greenhouse averaged 1600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD. Daily day/night greenhouse temperatures averaged 29 and 22°C, respectively. Shade treatments were applied on June 29, 1999, 21 d after planting. Black nylon mesh shade cloths were fitted to PVC frames to reduce light intensity to 60, 30, and 15% of available light (average of 960, 450, and 230 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD, respectively). The frames enclosed plants on all sides at a height of 1.5 meters. Twenty pots of each species were randomly placed under each frame so there was one treatment per bench, with 40 pots (divided into two rows) for a total of 160 pots. An additional 10 pots of each species were planted for a pretreatment baseline harvest. Shade treatments were randomly assigned to a bench and no significant light or temperature gradients were measured among the benches.

For baseline values, 10 replicates of each species were harvested from each of the four treatments at 21 d after planting (before initiation of treatment). Plant height, number of leaves, and number of stem tillers were measured and then plants were clipped at the soil surface, dried and weighed. For the pretreatment baseline harvest, the plants were very small so whole plants were used for leaf area determination. After measurements were taken in the subsequent 4- and 8-wk harvests times, but only the 8-wk harvest data are presented. Entire plants were removed from the soil and the roots were excised from the shoots. The leaf blades were then separated from the sheaths and culms at the collar. Roots were washed free of soil, and above and below ground plant parts were dried at 32°C for 48 hr before weighing. Leaf blades separated from the shoots at the collar were analyzed for leaf area as

described above, then dried and weighed. Only data from 8-wk harvest are presented.

Moisture stress. Moisture experiments were initiated 39 d after planting. All pots were watered to excess with tap water and allowed to drain overnight. Species were randomly assigned one of four drought treatments with 12 replicated pots per treatment. One treatment included a fully watered control. Control plants were measured at each new drought period to serve as an indicator of unstressed growth. Plants exposed to intermediate drought stress were not watered for 6 d, watered each day for 8 d, then again not watered for an additional 27 d. Plants exposed to a sustained drought period did not receive any additional water for 41 d. In the fourth treatment, plants were not watered for 12 d, watered once, and then allowed to dry until they became necrotic. These plants were used to obtain lethal water content (LWC). Plant height, number of leaves, and the number of stem tillers were measured in all plants.

It was not possible to determine the effects of the different drought periods directly on soil water potential because normal soils tensiometers are only useful in the range from 0.0 to −0.08 MPa (Kramer and Boyer 1995) and moisture levels in this experiment fell well below this range. Consequently, the relative water content (RWC) was determined in a subset of the replicates.

After the final growth measurements in all twelve replicates, six plants of both species were used to determine the effect of different drought periods directly on plant water status in each treatment. The remaining six replicates in each treatment were returned to container water capacity and monitored for survival and recovery for one week.

For the RWC analysis, the above ground plant was cut at soil level and immediately weighed. After weighing, the entire plant was placed under water and a fresh cut was made on the basal stems, and the entire plant was placed in a plastic bag filled with distilled water and allowed to saturate in a cool, dark chamber. After 24 hr, each plant was removed from the water, patted dry, and reweighed. The plants were then placed in an oven for 24 hr at 32°C before obtaining the final dry weight. RWC was determined according to the formula from Kramer and Boyer (1995):

$$RWC = \text{Fresh weight at harvest} - \text{Dry weight/} \\ \text{Saturated weight} - \text{Dry weight}$$

Lethal water content (LWC) was determined for plants that had become necrotic according to the formula:

$$LWC = \text{Fresh weight at harvest} \\ - \text{Dry weight/Dry weight}$$

In a second moisture stress experiment, pots containing twelve-wk-old seedlings were fully watered and allowed to drain for 24 hr. The soil surface was

sprinkled with 50 g of sand to prevent crusting and cracking during the drought treatment and the pot, plant, and soil were weighed to obtain an initial pot weight at container capacity. Container capacity (23% water ± 4%) was previously determined as the average amount of water remaining in the pot (10 replicates) after gravity drainage according to the method of Singer and Munns (1996). We recognize that container capacity in pot experiments may not be the same as field capacity because capillary columns are often shorter in pots than in field conditions (Kramer and Boyer 1995). However, the relative differences among treatments should provide an approximation of field conditions.

In this experiment, full light intensity in the greenhouse averaged 900 μmol·m^{-2}·s^{-1} PPFD. Daily day/night greenhouse temperatures averaged 22 and 17°C, respectively. Because of the timing of this experiment (November 1, 2000), light levels were significantly lower than the light intensity experiment conducted during the summer (June 29, 1999).

Prior to initiating treatments, six replicates per species were evaluated as previously described and harvested to obtain pretreatment baseline values for plant height, dry weight, and number of leaves. Seven replicates per species were randomly assigned to one of four moisture treatments: 1) 100–75%, 2) 75–50%, 3) 50–25%, and 4) less than 25% of container capacity, as determined by fractions of the initial pot weight. During the experiment, pots were allowed to dry to the low end of their container capacity range. This corresponded to 0, 5, 10, and 37 d without water for treatments 1, 2, 3 and 4, respectively. After the initial drying periods, plants were returned to the upper end of their container capacity range on a regular basis (usually every three days) by adding water to the pot until the initial pot weight was achieved. Plants were maintained under these moisture regimes for 8 wk before being harvested as previously described. Plant height, leaf number, leaf area and above ground biomass were evaluated.

Growth Analysis and Statistical Procedures

For seedling mortality values at various temperature conditions the individual replicates were analyzed between both species for each temperature using a chi-squared test (χ^2 value).

Mathematical growth analyzes were used to evaluate the effects of light and temperature on dry matter production and biomass partitioning into leaves, stems, and roots. Mean relative growth rate (RGR) was calculated for unpaired plants as the change in total dry weight over time (Evans 1972). For net assimilation rate (NAR), calculations were based on the formula from Causton and Venus (1981), which avoids the need to pair plants between harvests. NAR is calculated as the change in weight over time as a function of the assimilatory area. Leaf area ratio (LAR) was also calculated based on the formula from Evans (1972) as the relationship between leaf area and shoot dry weight. In the light experiment, a simple regression analysis was used for all data points and light was treated as a quantitative variable in order to evaluate the effects of light on biomass partitioning and relative growth rates. Graphs with regression curves include only means to simplify presentation.

Data for the two species were subjected to separate analyses of variance (ANOVA) to determine significant treatment effects. Scheffe's multiple comparison test was used to determine significant differences among the mean values for each species (P < 0.05). For each treatment, pairwise comparisons were made with Scheffe's test to determine if means differed significantly between the species (P < 0.05). The species effect was not tested between different treatments. All analyses were carried out using Statview® 5.1 software from SAS Institute Inc.

RESULTS

Temperature

Under growth chamber conditions, both *C. selloana* and *C. jubata* had significantly higher biomass at 20°C (Fig. 1). Growth was greatly reduced at both high and low temperature extremes. After 8 wk of temperature treatment, *C. selloana* seedlings had significantly greater height and leaf area compared to *C. jubata* at both 20 and 25°C (Table 1). At 20°C, *C. selloana* also had greater numbers of leaves and tillering stems than *C. jubata* (Table 1). There were no significant differences in the measured variables of the two species at all other temperatures.

The RGR of both species peaked at 20°C (Table 1). *Cortaderia selloana* grew significantly faster than *C. jubata* under optimal temperatures. The mean RGR of *C. selloana* was 74 and 67% greater than *C. jubata* at 20 and 25°C, respectively. Seedlings of *C. jubata* had a significantly greater leaf number (12.0), stem tiller number (1.9), leaf area (24.5 cm^2), RGR (1.7 mg g^{-1} day^{-1}), and dry weight (128 mg) growing at 15°C compared to seedlings growing at 25°C (8.0, 1.0, 12.9 cm^2, 0.9 mg g^{-1} day^{-1} and 53 mg, respectively), indicating an optimal temperature range of 15–20°C (Table 1 and Fig. 1). In contrast, the height, leaf number, leaf area, RGR, and dry weight of *C. selloana* seedlings at both 15 and 25°C were significantly lower compared to those at 20°C. Furthermore, the average height of *C. selloana* seedlings was nearly twice as high when grown at 25°C compared to 15°C. This suggests that optimal growth of *C. selloana* occurs at around 20°C.

While temperature did not significantly affect *C. selloana* survivorship, *C. jubata* mortality increased significantly at temperatures above 25°C. At these higher temperatures, survival of *C. jubata* seedlings
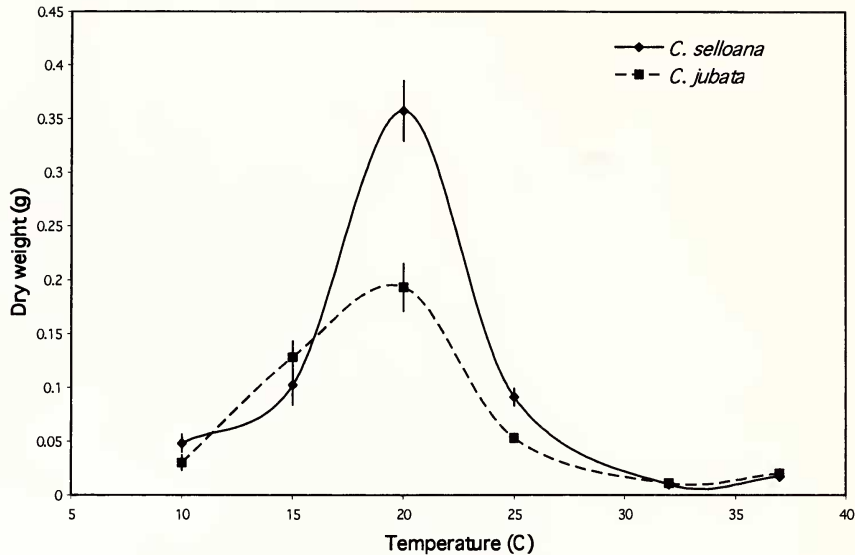
FIG. 1. Temperature effect on average dry weight of *C. selloana* and *C. jubata* under growth chamber conditions. Data are means ± SE.

was 10% or less, whereas *C. selloana* seedling survival was 63 and 52% at 32 and 37°C, respectively (Fig. 2).

Light

Vegetative growth and biomass partitioning. A regression analysis showed a linear increase in *C. selloana* RGR (roots and shoots) after 8 wk of growth as light intensity increased up to the maximum light level of 1600 μmol m^{-2} s^{-1} (Fig. 3). Average total dry weight of *C. selloana* seedlings reached 2.36 g under 1600 μmol m^{-2} s^{-1}, 65% higher than plants growing at 960 μmol m^{-2} s^{-1} (1.5 g) (Table 2). In contrast, *C. jubata* achieved optimal growth at 960 μmol m^{-2} s^{-1} (60% available light). Average *C. jubata* total dry weight was 1.02 g and did not increase with the additional light in the full sun treatment (Table 2). In addition, *C. jubata* plant height was significantly reduced under

high light intensity (33.1 cm) compared to seedlings exposed to lower light levels (average of 53.5 cm at three lower light levels) (Table 3). By comparison, light level did not significantly affect plant height in *C. selloana* (average height 67 cm).

Cortaderia selloana was more vigorous than *C. jubata* under high light conditions, producing nearly two and a half times as much biomass at full sun (Table 2). Leaf area, LAR, and NAR were also significantly greater in *C. selloana* at full sun compared to *C. jubata* (Table 3), but the number of tillering shoots and leaves was not significantly different at any light level (personal observation). Regardless of the light intensity, *C. selloana* seedlings were always significantly taller than *C. jubata*.

Growth analysis. For the growth interval from 0–8 wk, the RGR of *C. jubata* increased with increasing light intensity up to a maximum rate of 12.7 mg g^{-1} day^{-1} at 960 μmol m^{-2} s^{-1} (Fig. 3).

TABLE 1. EFFECTS OF TEMPERATURE (°C) ON GROWTH AND RELATIVE GROWTH RATES (RGR) OF *C. JUBATA* AND *C. SELLOANA* GROWN FOR 8 WEEKS UNDER GROWTH CHAMBER CONDITIONS. Pooled results from northern and southern California populations are shown for *C. jubata*. Results are presented only for 15, 20 and 25°C. No statistical differences were measured among growth parameters of the two species at all other temperatures. Each data point represents the mean of at least 12 replicates. * Within each column, different letters indicate a significant difference (P ≤ 0.05) among temperature treatments within a species according to Scheffe's multiple comparison test. Bolded and italicized values indicate significant difference (P < 0.05) between the two species.

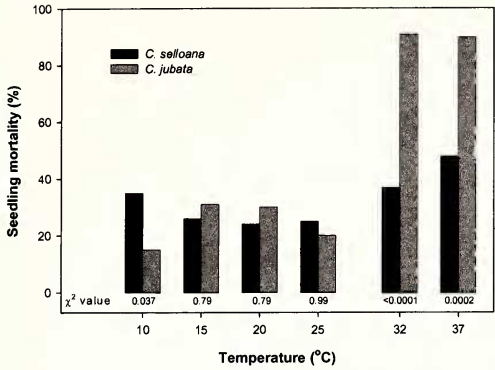| Species	Temperature (°C)	Height (cm)	Leaf no.	Tiller no.	Leaf area (cm^2)	RGR (mg g^{-1}·day^{-1})
C. jubata	15	25.3 b*	12.0 a	1.9 a	24.5 a	1.7 b
	20	*41.7* a	*10.1* ab	*1.3* b	*32.3* a	*3.1* a
	25	*24.8* b	8.0 b	1.0 c	*12.9* b	*0.9* c
C. selloana	15	25.5 c	11.2 b	2.1 a	21.1 b	1.9 b
	20	*63.0* a	*16.2* a	*2.8* a	*53.1* a	*5.4* a
	25	*44.3* b	8.2 b	1.1 b	*23.2* b	*1.5* b

FIG. 2. Percent mortality of *C. selloana* and *C. jubata* seedlings after 8 weeks in the growth chamber. Each species was initially represented by 25 to 50 seedlings at each temperature. Chi squared values for significance are indicated below the bars.

The RGR did not increase further at full available sunlight (1600 μmol m^{-2} s^{-1}). A similar pattern was seen in net assimilation rate (NAR) (Table 3). The leaf area ratio (LAR) remained constant between 60 and 100% light intensity, indicating that plants reached photosynthetic light saturation (Table 3).

In contrast, the RGR of *C. selloana* increased linearly with increasing light intensities (Fig. 3). Seedlings with full available sun reached a maximum growth rate of 21.4 mg g^{-1} day^{-1} (70% greater than *C. jubata*) over the growth interval from 0–8 wk. When light intensity increased from 960 to 1600 μmol m^{-2} s^{-1} a decline in LAR was apparently offset by a 36% increase in NAR, which reached a peak value of 3.04 mg cm^{-2} day^{-1} at full sun (Table 3). Thus, the RGR continued to increase as light intensity increased and *C. selloana* did not reach a light saturation point. This indicates that

C. selloana seedlings adjusted to high light conditions through increased photosynthetic efficiency. Consequently, *C. selloana* seedlings in full sun were more physiologically active than *C. jubata* and attained a much greater size.

Drought

Moisture is often a critical factor in plant establishment in the Mediterranean climatic regions of California. Protracted summer drought makes it difficult for young seedlings to survive to maturity. Both species demonstrated high drought tolerance in the greenhouse experiments, with some seedling plants of each surviving up to 41 d without water. The drought treatments significantly reduced the RWC of 12 wk old seedlings. Fully watered controls of both species had an average RWC greater than 88%. Moderate drought reduced the RWC to 47.4% and 41.8%, and sustained drought to 28.4% and 31.8%, for *C. jubata* and *C. selloana*, respectively.

Drought significantly reduced growth of both species, but *C. selloana* was more tolerant of moderate drought than *C. jubata* (Fig. 4). The mean dry weight of 12 wk old *C. selloana* seedlings was twice that of *C. jubata* (0.75 g compared to 0.37 g) when water was withheld for 27 d. Average dry weight of moderately stressed plants was 55% lower than control plants in *C. jubata*, compared to a 33% reduction in *C. selloana*. This difference corresponded to the pattern of leaf production. Under moderate drought, *C. jubata* leaf production declined 50%, from 18 leaves per plant in the full water treatment to only 9 leaves per plant in the 27 d drought period (Fig. 5). In contrast, moderate drought did not significantly affect *C. selloana* leaf production, both fully watered and moderately stressed plants had between 12–13 leaves. Drought
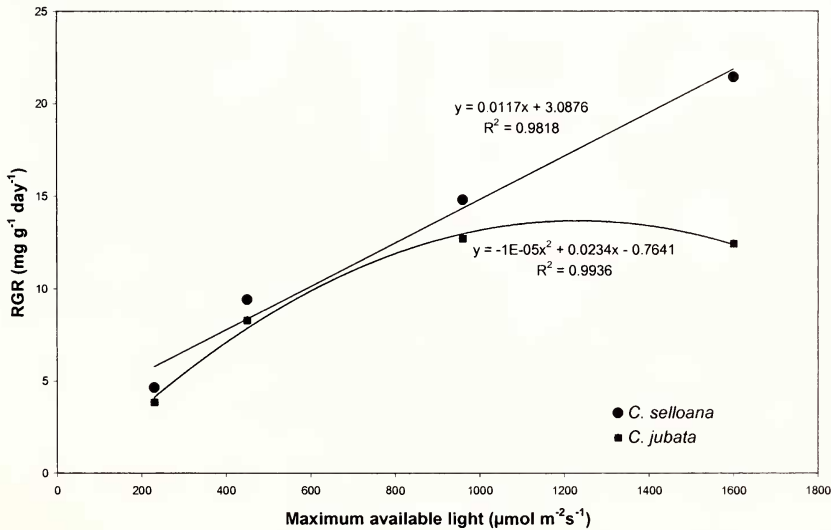

FIG. 3. Light effects on relative growth rates (RGR) of *C. selloana* and *C. jubata* after 8 wk of treatment.

TABLE 2. EFFECTS OF LIGHT ON *CORTADERIA* ROOT, LEAF AND SHOOT, AND TOTAL DRY WEIGHT AFTER 8 WEEKS IN THE GREENHOUSE. Each data point represents the mean of 10 replicates. * Within each column, different letters indicate a significant difference (P ≤ 0.05) among light treatments within a species according to Scheffe's multiple comparison test. Bolded and italicized values indicate significant difference (P < 0.05) between the two species.

Species	Light (μmol m^{-2} s^{-1})	Root dry wt (g)	Shoot and leaf dry wt (g)	Total dry wt (g)
C. jubata	230	0.06 b*	0.19 c	0.25 c
	450	0.25 b	0.36 b	0.61 b
	960	0.59 a	*0.43* a	1.02 a
	1600	*0.56* a	*0.45* a	*1.01* a
C. selloana	230	0.06 c	0.26 c	0.31 d
	450	0.26 c	0.48 b	0.74 c
	960	0.72 b	*0.71* a	1.43 b
	1600	*1.42* a	*0.94* a	*2.36* a

also reduced average plant height in both species but *C. selloana* was significantly taller than *C. jubata* even in the control plants not exposed to drought (Fig. 6).

Stem tiller number, LWC (amount of water remaining in plants at necrosis), and mortality were not significantly different between the two species. The LWC of *C. jubata* and *C. selloana* was 0.13 ± 0.05 and 0.16 ± 0.08 g, respectively. Based on the similar LWC values, mortality rates were expected to be similar. Mortality of *C. selloana* and *C. jubata* after 41 d of sustained drought was 33 and 42%, respectively.

Soil Moisture Content

After 8 wk, soil moisture regimes greater than 25% container moisture capacity did not significantly affect RGR of either species. Relative growth rates of 20 wk old seedlings averaged 11.7 mg g^{-1} day^{-1} and 13.9 mg g^{-1} day^{-1} in *C. jubata* and *C. selloana,* respectively, when soil moisture content was greater than 25% (Table 4). Despite similar growth rates, *C. selloana* seedlings grew significantly taller and had significantly higher leaf area and average dry weights than *C. jubata* at the two moderately moisture conditions (50 and 75%). At these soil moisture ranges, *C. selloana* plants

were on average 77 cm tall, with 100.5 cm^2 leaf area, and 1.66 g dry weight while *C. jubata* plants averaged 62.5 cm tall, 82 cm^2 leaf area, and only 1.34 g dry weight (Table 4). Leaf and tiller counts were not significantly different in any treatment.

Only severe soil moisture depletion at <25% soil moisture lowered relative growth rates and reduced plant height and dry weight in both species. The average dry weight of *C. selloana* and *C. jubata* seedlings at 25% soil moisture was 67 and 64% lower, respectively, than the combined average for soil moistures above 25%. This suggests that beyond this minimum threshold, water availability is not limiting plant growth.

DISCUSSION

This study suggests that a combination of physiological and morphological factors make *C. selloana* potentially more invasive than *C. jubata.* Based on these results, *C. selloana* growth is more vigorous then *C. jubata* under optimal conditions. *Cortaderia selloana* demonstrated greater survivorship at high temperatures, an ability to utilize higher light intensities, and greater drought tolerance than *C. jubata.*

Temperature is one of the most important environmental factors limiting the geographic distribu-

TABLE 3. EFFECTS OF LIGHT ON *CORTADERIA* HEIGHT, LEAF AREA, LEAF AREA RATIO (LAR = LEAF AREA/TOTAL PLANT DRY WT), AND NET ASSIMILATION RATE (NAR = PLANT GROWTH RATE/DAY) AFTER 8 WEEKS IN THE GREENHOUSE. Each data point represents the mean of 10 replicates. * Within each column, different letters indicate a significant difference (P ≤ 0.05) among light treatments within a species according to Scheffe's multiple comparison test. Bolded and italicized values indicate significant difference (P < 0.05) between the two species.

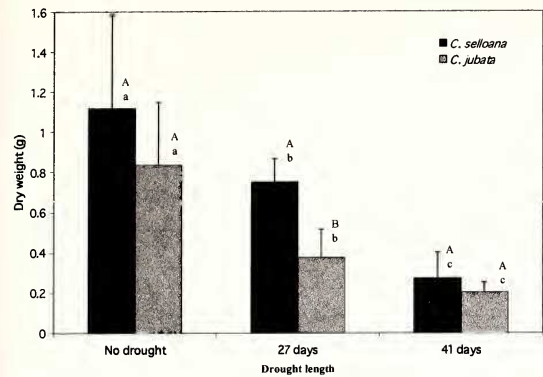| Species	Light (μmol m^{-2} s^{-1})	Height (cm)	Leaf area (cm^2)	LAR (cm^2 g^{-1})	NAR (mg cm^{-2} day^{-1})
C. jubata	230	*56.1* a*	36.6 a	144.4 a	0.61 c
	450	*56.8* a	51.4 a	86.8 b	1.01 b
	960	*47.5* a	48.5 a	48.5 c	1.85 a
	1600	*33.1* b	*46.3* a	*46.3* a	*1.91* a
C. selloana	230	*67.8* a	41.8 b	134.9 a	0.54 d
	450	*73.4* a	53.1 ab	73.1 b	1.16 c
	960	*70.3* a	60.7 ab	46.9 c	1.96 b
	1600	*60.1* a	*69.7* a	*28.7* d	*3.04* a

FIG. 4. Effect of drought on average dry weight of *C. selloana* and *C. jubata* under greenhouse conditions. Bars represent standard deviation. Upper case letters differing within each treatment represent significant difference (P < 0.05) between the two species. Lower case letter differing among treatments represent significant differences within a species.
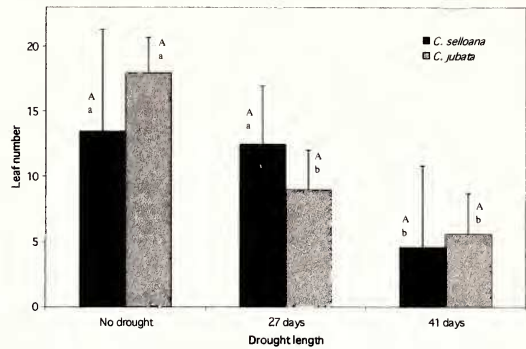

FIG. 5. Effect of extended drought on leaf number in *C. selloana* and *C. jubata*. Bars represent standard deviation. Upper case letters differing within each treatment represent significant difference (P < 0.05) between the two species. Lower case letter differing among treatments represent significant differences within a species.

tions of plants, determining the time of year during which growth and reproduction may occur, and regulating rates of plant growth and development (Patterson 1985). The greater temperature tolerance of *C. selloana* probably contributes to its success as an ornamental, as well as its invasive potential, in inland areas. In addition, it may provide an explanation for its concentrated distribution in southern California. Although young seedlings growing actively in the spring are unlikely to experience these high temperatures under natural conditions, the apparent inability to withstand high temperatures may partially explain why *C. jubata*, but not *C. selloana*, is restricted to coastal areas (particularly central and northern) and has failed to establish in inland sites. Young *C. jubata* may not be able to tolerate high summertime temperatures common in interior regions of the state (mean daily maximum temperature in Sacramento, CA, in July is 34°C).

DiTomaso et al. (1999) and Lambrinos (2001) determined that *C. selloana* is the dominant *Cortaderia* species along the California coastline south of Santa Barbara County. The southern coast has less fog and higher temperatures (mean daily maximum in San Diego is 27°C) than the central and north coast of California. In northern California, typical coastal temperatures in the summer are close to the optimal temperature for both species (mean daily maximum in Monterey in July is 20°C), and in these areas both species co-occur.

The distribution pattern of both species may also be related to frost tolerance. Although no studies have compared the survival of either species at extremely low temperatures, Costas-Lippmann (1976) observed that an unusual, prolonged frost in Berkeley, CA, severely injured adult *C. jubata* plants, (although they were not killed) but did not harm *C. selloana* adults. Frost is relatively uncommon in coastal California but does occur regularly in the interior regions of the state. For example, coastal Monterey County averages only two frost days per year, while Sacramento experiences an average of 18 frost days per year (http://www.weatherbase.com/weather/city.php3?c=US&s=CA&refer=).

Maximum growth of many plant species occurs at full light intensity and growth rates decrease as irradiance is reduced (Radosevich et al. 1997). Morphological responses to decreased light intensity can include reduced tillering, decreased root growth, and lower relative growth rates (Patterson 1985). Low light conditions significantly reduced plant weight, leaf area, and NAR in both *Cortaderia* species. Other studies have documented similar responses to shade in grass species including *Sorghum halepense* (McWhorter 1976), *Rottboellia exaltata* (Patterson 1979), and *Imperata cylindrica* (Patterson 1980). Seedling response in the two species growing with 70 or 85% light reduction were
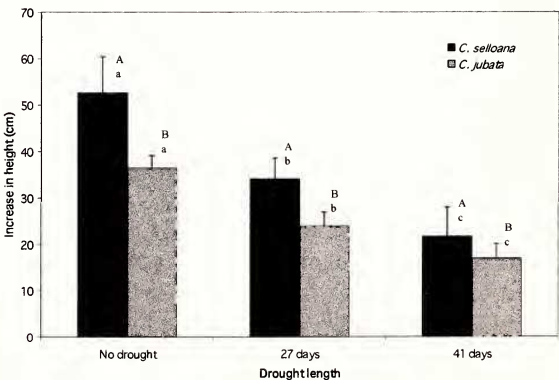

FIG. 6. Effect of extended drought on plant height in *C. selloana* and *C. jubata*. Bars represent standard deviation. Upper case letters differing within each treatment represent significant difference (P < 0.05) between the two species. Lower case letter differing among treatments represent significant differences within a species.

TABLE 4. EFFECT OF SOIL MOISTURE ON MEAN PLANT GROWTH OF *C. JUBATA* AND *C. SELLOANA* AFTER 8 WEEKS AT FOUR CONTAINER WATER CAPACITIES. Each data point represents the mean of 12 replicates. * Within each column, different letters indicate a significant difference ($P \leq 0.05$) among water treatments within a species according to Scheffe's multiple comparison test. Bolded and italicized values indicate significant difference ($P < 0.05$) between the two species.

Species	Percent container water capacity	Height (cm)	Leaf area (cm²)	Total dry wt (g)	RGR (mg g⁻¹ day⁻¹)
C. jubata	25	37 b*	14 c	0.43 b	5.4 b
	50	*61* a	*61* b	*1.25* a	11.3 a
	75	*64* a	*103* a	*1.43* a	12.9 a
	100	*63* a	104 a	1.24 a	11.0 a
C. selloana	25	58 b	*27* c	0.61 b	6.8 b
	50	*74* ab	*84* b	*1.71* a	14.1 a
	75	*80* a	*117* a	*1.61* a	13.5 a
	100	*81* a	127 a	1.75 a	14.1 a

nearly identical, with the exception of plant height. Although growth rates were similar in low light, *C. selloana* appears to have an advantage over *C. jubata* in closed canopies because it grows taller, enabling seedlings to grow through existing vegetation sooner to capture more light. The greater size of *C. selloana* may also facilitate encroachment into undisturbed areas.

High growth rates and biomass production of *C. selloana* seedlings under high light conditions can also contribute to the success of *C. selloana* as an ornamental in inland areas. *Cortaderia selloana* seedlings in the greenhouse did not reach a light saturation point, indicating that plants are able to utilize the higher light conditions typical of warm, sunny inland regions of California. In contrast, *C. jubata* apparently reaches maximal growth in moderate light intensities (960 μmol m⁻² s⁻¹) that are more typical in coastal regions with frequent fog and cloud cover.

Although moisture does not appear to be a limiting factor for either species in coastal regions, water availability may restrict *C. selloana* distribution in hot dry climates. With the exception of dense urban areas like the San Francisco Bay Area, where the two species co-occur, coastal infestations in northern California are primarily *C. jubata,* while *Cortaderia* infestations south of Santa Barbara are generally dominated by *C. selloana.*

Lambrinos (2002) suggested that *C. selloana* has a greater ability than *C. jubata* to use available water. He transplanted seedlings in the field between various plant community types and found no growth differences between the species except in seasonal wetlands, where *C. selloana* seedlings had greater leaf area and survivorship. In this moisture experiment, leaf area was also the most sensitive growth parameter to changes in moisture level. In both species, leaf area was reduced when field capacity dropped below 50%, but plant height and dry weight were not reduced until field capacity was less than 25%. In our experiment, average leaf area dropped by 41% in *C. jubata* and 32% in

C. selloana when moisture content dropped from 75% to 50%.

More vigorous root development in *C. selloana* seedlings growing with high light intensity may account for its ability to more effectively capture water and nutrient resources than *C. jubata*. Under high light conditions in the greenhouse (960 μmol m⁻² s⁻¹), *C. selloana* did not reach light saturation. With the majority of plant biomass stored in the roots, high growth rates would enable *C. selloana* roots to use up available water more quickly. This may explain why *C. selloana* is restricted to areas with plentiful water in inland areas, such as riparian zones and wetlands. Moisture likely becomes the limiting factor to plant growth when both light and temperature are high in the summer. However, results from this experiment suggest that under moderate temperature and light conditions, like those of the foggy northern California coast, moisture is not a limiting factor.

Although these experiments suggest that the distribution patterns of both *Cortaderia* species in California is based on physiological and morphological factors, it is also plausible that the distribution patterns of both species are related to differences in introduction patterns. It is possible that both species have not yet reached their potential distributions within the state, and their current distribution is based on human dispersal factors, primarily associated with the nursery trade. Although unlikely, it is possible that over a longer time period, both species may co-occur throughout the coast as well as in interior ecosystems. This, however, is more difficult to determine with *C. jubata,* since its history of introduction is not as well documented as that of *C. selloana.*

It is possible that the greater genetic diversity and observed ecotypic plasticity in *C. selloana* is the result of repeated horticultural introductions. Multiple introductions may substantially accelerate the spread of invasive plants from horticultural origin (Reichard and Hamilton 1997). Humans can disperse plants long distances throughout California

and adjacent states, generating multiple foci for spread. Imported horticultural material supplies genetic inputs and may introduce more adaptive traits or higher fertility cultivars. Continued sale and distribution of both male and female forms of *C. selloana* may increase the threat of spread through enhanced reproductive output.

Based on these result, detection efforts should focus on *C. selloana* in more inland, particularly riparian areas and wetlands, environments. Should new invasions be detected in these areas, the highest priority should be given to populations consisting of both functionally male and female plants. Preventing further expansion of newly established populations will depend upon rapid response prior to viable seed development.

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